Secondary succession through non-native dicotyledonous woody plants in New Zealand

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(Received October 14 2010, revised and accepted 16 April 2011)

Abstract

Thirty-six species or species groups of non-native dicotyledonous woody plants found in New Zealand and that are considered to occur at a landscape scale (i.e., in patches of greater than 80% cover and that exceed 0.25 ha in area) are listed and reviewed with regard to their potential for enabling secondary succession by native vegetation. Of the 36 introduced species, 14 are described as being replaced by native species in some circumstances (e.g., *Buddleja davidii*, *Calluna vulgaris*, *Cytisus scoparius*, *Hakea* spp., and *Ulex europaeus*). A further 8 species are reported to have native seedlings beneath the canopy, but it is still too premature to determine whether these will replace the non-native species (e.g., *Acer pseudoplatanus*, *Berberis* spp., and *Salix* spp.). However, the remaining 14 species have no records of either being replaced or having native species beneath their canopies. Two of these species are short-lived shrubs (*Lantana camara* and *Teline monspessulana*) that will probably be replaced by native species in some circumstances, although no published records of this occurring are currently available. In contrast, *Ligustrum lucidum* and *Rhamnus alaternus* are predicted to be persistent for the foreseeable future, and this may also apply to the hard-seeded legumes (e.g., *Ulex europaeus* and *Cytisus scoparius*) in frequently disturbed habitats.

Key words: non-native woody plants - dicotyledons - introduced species - plant interactions - vegetation succession - native regeneration - New Zealand.

Introduction

Several non-native woody species have dominated large areas of New Zealand for decades (Blaschke *et al.* 1981; Bascand & Jowett 1981), while others have become problematic more recently (Cameron 1990; Howell 2008). Many of these species now occur at a landscape scale (i.e., in patches of greater than 80% cover and that exceed 0.25 ha in area). The increasing abundance of these introduced species has meant many appear as pest plants in Regional Council Pest Management strategies, while at the same time, their role in vegetation restoration is also gaining attention (Meurk & Hall 2006; Walker *et al.* 2003). However, whether they are treated as noxious weeds or steps to indigenous landscapes depends partly on the management objectives for the localities where they grow, but also on whether or not their role in vegetation succession is well understood by land

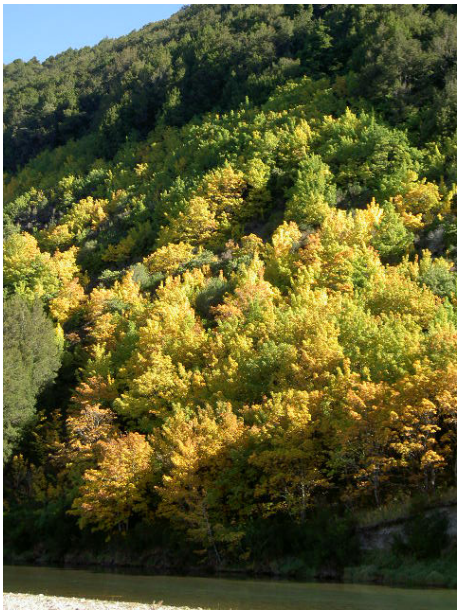

Figure 1. Sycamore is widespread in western Southland and Otago, seen here invading native scrub in the upper Mataura. The future of this vegetation is unknown.

managers (Williams 1997). A summary of the role such plants provide was published 18 years ago (McQueen 1993), although it only mentioned 15 species present at the landscape scale. Similarly, Wardle (1991) also made scattered observations of vegetation succession. It is therefore timely to compile a record of the information currently available including that in university theses and technical reports. This record is augmented with the author's own unpublished observations where relevant.

Methods

The 36 species or species groups listed (Table 1) are those occurring at a landscape scale in New Zealand (i.e., in patches of greater than 80% cover and that exceed 0.25 ha in area) or that have the potential do so in the next 30 years (author, pers. obs.). Such attributes make these plants of interest to both scientists and land managers. However, it should be noted that there are many recently naturalised plants that have not been included. In addition, conifers are omitted because they have been well summarised by Ledgard and colleagues (Paul & Ledgard 2008).

In this article, the species or species groups are summarised individually in the alphabetical order of their Latin names. Species such as gorse (*Ulex europaeus*) and broom (*Cytisus scoparius*) are notable with 10 and 7 references respectively dealing with their role in vegetation succession. In contrast, there are 53 references dealing with the other 34 species mentioned (Table 1). Species for which no literature could be found are not listed in the main body of the text.

The literature cited and the author's observations are largely confined to field observations made in New Zealand. The year that the species was first recorded in the wild (Webb *et al.* 1988), their life-form, and seed dispersal mechanism is initially stated in all instances. Certain references on shade tolerance or physiology are given where they are pertinent to the species persistence, but this article is not intended as an autecological summary. In consideration of the summary already given by McQueen (1993), the author has attempted to update and augment the information provided by this work, although in some instances, the reader is referred to this article for greater detail on some of the more common species.

Acer pseudoplatanus (sycamore)

This wind-dispersed tree was first recorded in 1880 (Webb *et al.* 1988). It has been widely planted as an ornamental or for firewood, and is common on forest margins and in open areas, particularly from Canterbury (e.g., Peel Forest; author, pers. obs.) to Otago (e.g., Kawarau Gorge; Johnson 1985) and Southland

(Williams 2009).

In northern Southland (Figure 1), sycamore invades regenerating native and non-native scrub and appears to be preventing the expansion of the adjacent beech (*Nothofagus* spp.) forest, although it does not invade beneath a closed beech canopy (Williams 2009). Some of these stands have been established for 30 years or more, but it is still too premature to enable an accurate prediction of vegetation composition in the future.

Sycamore stands at Peel Forest, Canterbury, have seedling native conifers (author, pers. obs.) but whether they will replace sycamore is unknown. Meurk & Hall (2006) produced models of forest dynamics for Christchurch and Queenstown that indicated sycamore would persist in the landscape for centuries; but because the data is not derived from New Zealand, the veracity of these predictions remains uncertain.

***Berberis darwinii* (Darwin's barberry)**

This fleshy-fruited, spiny-leaved shrub was first recorded in 1946 (Webb *et al.* 1988) and is now common throughout the lower North Island and South Island. It is commonly up to 5 m tall in marginal situations and canopy gaps but adult trees are relatively shade-tolerant and can reach 15 m damaged forests (Allen 1991). Juveniles have been found in closed-canopy pine plantations (Moles & Drake 1999). Where it has developed relatively dense stands in abandoned pasture, seedlings of native species appear once Darwin's barberry reaches 2 to 3 m tall (Keller 1983). However, McQueen (1993) noted that there are no chronological studies of succession through Darwin's barberry. This meant that it was not possible to explain its presence in taller forests as having persisted since early establishment in more open conditions, or whether it actively invades intact forest. However, experimental studies suggest the latter is unlikely because seedlings are not highly-shade tolerant and can establish only on forest edges or in canopy gaps (McAlpine & Jesson 2007).

***Berberis glaucocarpa* (barberry)**

This fleshy-fruited, spiny-leaved shrub was first recorded in 1916 (Webb *et al.* 1988) and is now common throughout the North Island and upper half of the South Island. It is very common in Nelson where it often replaces gorse and other shrubs (Sullivan *et al.* 2007). Hall's totara (*Podocarpus hallii*) saplings have been observed beneath tall barberry scrub in Nelson and these may eventually replace the barberry (author, pers. obs.).

***Buddleja davidii* (buddleia)**

Buddleia is a multi-stemmed wind-dispersed shrub, first recorded in 1946 (Webb *et al.* 1988). It is widespread on disturbed ground throughout New Zealand. The summary of published and unpublished information by McQueen (1993) indicates that in parts of the North Island, buddleia can dominate early in successions on fresh alluvium. Where the surface remains stable, and buddleia establishes en masse, all other plants are initially shaded out, including native pioneers such as tawhinu (*Ozothamnus leptophylla*) and tree tutu (*Coriaria arborea*), both which reach approximately the same age, and kanuka (*Kunzea ericoides*), which lives for much longer than buddleia. Because stands of the latter are overtaken by native broad-leaved woody species in less than 50 years, the return to native mixed hardwood forest through buddleia is therefore accelerated over the succession through kanuka

Table 1. Non-native woody plants, other than conifers[1], that (a) occur as the dominants (>80% cover) in patches covering at least 0.25 ha, or (b) may do so in the next 30 years (author, pers. obs.). The number of references refers only to those New Zealand sources concerning their role in vegetation succession.

Scientific name	Common name	Coverage	No. references[2]
Acer pseudoplatanus	sycamore	a	2
Berberis darwinii	Darwin's barberry	a	4
Berberis glaucocarpa	barberry	a	1
Buddleja davidii	buddleia	a	5
Calluna vulgaris	heather	a	3
Cotoneaster spp.	cotoneaster	a	
Chrysanthemoides monilifera spp. *monilifera*	boneseed	a	1
Crataegus monogyna	hawthorn	a	3
Cytisus scoparius	broom	a	7
Elaeagnus x *reflexus*	elaeagnus	a	
Erica lusitanica	Spanish heath	a	4
Hakea gibbosa	downy hakea	a	4
Hakea salicifolia	willow-leaved hakea	a	1
Hakea sericea	spiny-leaved hakea	a	4
Lantana camara	lantana	a	2[2]
Leycesteria formosa	Himalayan honeysuckle	a	3
Ligustrum lucidum	tree privet	a	2
Ligustrum sinense	Chinese privet	a	1
Lupinus arboreus	tree lupin	a	1
Lycium ferocissimum	boxthorn	a	1
Paraserianthes lophantha	brush wattle	a	
Prunus serrulata (and others)	Japanese cherry	b	
Pyracantha angustifolia	firethorn	b	
Racosperma dealbata	silver wattle	a	
Racosperma longifolia	Sydney golden wattle	a	1
Racosperma mearnsii	black wattle	a	1[2]
Rhamnus alaternus	evergreen buckthorn	a	1[2]
Rhododendron ponticum	rhododendron	a	
Rosa rubiginosa	sweet briar	a	3
Salix cinerea	grey willow	a	1
Salix fragilis	crack willow	a	1
Sambucus nigra	elder	a	2
Solanum mauritianum	woolly nightshade	a	1[2]
Sorbus aucuparia	rowan	b	
Teline monspessulana	Montpellier broom	a	
Ulex europaeus	gorse	a	10

1 = For conifers, see Paul & Ledgard (2008)
2 = Summary observations, not site-specific (e.g., Esler 1988)

(Smale 1990).

However, this simple successional model through buddleia does not necessarily apply where it establishes together with native shrubs. Buddleia occurred with kanuka and manuka (*Leptospermum scoparium*) on the youngest surfaces in the Orongorongo valley, Wellington, where it was outcompeted by these native shrubs in 20 years (Gibb 1994). Similarly, in riverbed successions at Kaikoura, tree tutu overtops buddleia (Dobson 1979). Detailed studies by Bellingham *et al.* (2005) in the same area reported no evidence for potential facilitation or competition between buddleia and tree tutu, nor for any species diversity measure declining with buddleia biomass. Possibly their stands had not reached the stage age reported by Dobson (1979) where the two species were competing. Mixed stands of buddleia and tree tutu were present in the Urewera National Park but they were not sampled (Smale 1990).

Instability brought about by flooding results in a return to buddleia (e.g., in the Orongorongo valley; Gibb 1994) and so buddleia is likely to persist within individual catchments, irrespective of individual stand dynamics.

Calluna vulgaris (heather)

This short wind-dispersed shrub was first recorded in 1910 (Webb *et al.* 1988). The most extensive invasions of heather are in the Tongariro National Park, central North Island. McQueen (1993) noted that up to an elevation of 1200 m a.s.l. and where the stands were not completely closed, heather was being overtopped by manuka. The timing of succession from a heather-dominated plant community to one characterised by manuka and inaka (*Dracophyllum longifolium*) is dictated by time since the last fire, topography, and elevation (Rogers & Leathwick 1996). On side slopes at 900 metres a.s.l., native species exceed the cover of heather 38 years after burning, while on crests it takes 60 years and on basin floors at least 75 years for native species to replace heather (Rogers & Leathwick 1996). At 1100 metres a.s.l, or on sites influenced by cold air drainage and/or waterlogging, the process takes much longer, and heather may even be considered a permanent feature where it establishes above the tree line (Chapman & Bannister 1990). Despite this, there is no basis for comparing the influence of heather on successional patterns and rates of change because vegetation dynamics in its absence has not been described (e.g., Rogers & Leathwick 1996).

Chrysanthemoides monilifera spp. *monilifera* (boneseed)

This short fleshy-fruited shrub was first recorded in 1870 (Webb *et al.* 1988) and has spread actively in coastal New Zealand over the last 30 years (author, pers. obs.). Native seedlings have been found beneath boneseed in the Wellington area, but estimating successional trajectories was not possible (McAlpine *et al.* 2009). Boneseed has been extensively studied in Australia because of its ability to invade a wide range of open vegetation (e.g., Weiss *et al.* 1998).

Cotoneaster spp. (cotoneaster)

Webb *et al.* (1988) list seven species of these fleshy-fruited shrubs, all of them first reported in 1940 or later. There have been no studies regarding this groups role in vegetation succession. However, their abundance appears to have increased in the last 20 years to the extent that they are mentioned in 18 notes published in the New Zealand Botanical Society Newsletter from 1993 onwards (e.g., Ogle & Sykes 2003), and the potential for the

control of silver-leaved cotoneaster (*C. pannosus*) was recently discussed by Webb (2009). Khasia berry (*C. simonsii*) in the South Island was reported by Webb *et al.* (1988) as being distributed from Hamner southwards, but since then it has spread into the main valleys found north of this locality (author, pers. obs.). Its upright growth habit (Webb *et al.* 1988) enables it to penetrate through dense blackberry (*Rubus fruticosus* agg.) and broom stands. It forms particularly dense stands (e.g., those near Turangi township on the Volcanic Plateau), and they appear to have not changed over a period of 20 years (author, pers. obs.).

Crataegus monogyna (hawthorn)

This fleshy-fruited small tree was first recorded in 1899 (Webb *et al.* 1988) is now widespread, particularly in the eastern regions of the South Island (e.g., Bascand & Jowett 1981). In the lowlands, it readily establishes on forest margins and in damaged forest but as it is shade-intolerant, it does not persist after canopy closure by taller native trees (Williams & Buxton 1986). In contrast, at higher elevations from Marlborough to Southland, it is spreading from numerous loci in areas between 200-600 metres a.s.l. with c. 750-1500 mm precipitation (Bascand & Jowett 1981). In Otago, hawthorn is most frequent in associations characterised by broom-gorse shrublands (Walker *et al.* 2003). At Porters Pass, Canterbury, it has spread through matagouri (*Discaria toumatou*) scrub (Williams & Buxton 1986). During more recent studies at the same Porters Pass site, scattered seedlings of relatively shade-tolerant native broadleaf (*Griselinia littoralis*) were observed beneath old hawthorn trees, and in the absence of grazing, hawthorn may eventually be succeeded by broadleaf forest (Williams *et al.* 2010).

Cytisus scoparius (broom)

This small-leaved shrub was first recorded in 1872 (Webb *et al.* 1988). It has explosive capsules producing long-lived seeds. It is already widespread in New Zealand, but wide areas of inland South Island are still vulnerable to invasion and its spread continues in many areas. In the central North Island, native seedling establishment into broom stands occurs faster than into grass, but it may be slower than into native shrublands (Trass 2000). On previously forested sites with well developed soils, close proximity to native seed sources, and an absence of fire disturbance, broom is replaced by native vegetation. This can occur directly (Trass 2000), or in the South Island, through non-native bird-dispersed species such as elder (*Sambucus nigra*; Williams 1983). Replacement of broom would also be slow on thin stony soils subject to summer drought (Partridge 1992) or other climatic extremes (Smale *et al.* 2001). Broom can be replaced by tutu where they establish together on riverbeds if the sites remain undisturbed (Dobson 1979).

However, broom dominance persists in the absence of taller competitors over large areas of South Island braided riverbeds. Where matagouri and broom grow together, the long-term trend is likely to be governed by grazing pressure and fire (Bellingham 1998). Many of the extensive stands of broom in inland Marlborough and Canterbury (e.g., in the Clarence and Waiau valleys) appear to be self-perpetuating or developing into blackberry stands (e.g., west of Hamner), but to what extent this reflects merely an absence of a native seed source is unknown (author, pers. obs.). At localities with cooler temperatures, such as near Turangi and parts of the upper Waimakariri River catchment, broom appears to be replaced by Khasia berry (author,

pers. obs.).

Broom can form a nurse crop for taller non-native introduced trees such as sycamore (e.g., in the upper Mataura Valley, Southland; author, pers. obs.) and models of vegetation change in Otago show similar trends at some localities (Walker *et al.* 2009). Disturbance by fire, or substrate instability as on cliffs and riverbeds appears to result in the persistance of broom from the long-term seed bank (author, pers. obs.).

Erica lusitanica (Spanish heath)

This wind-dispersed nanophyllous small shrub was recorded in 1926 (Webb *et al.* 1988). It is common in wetter areas with acidic soils of both the North and South Islands. It commonly forms early successional vegetation with manuka and because of a long-term seed bank; it can persist for longer than the former in the presence of repeated fires (Mather & Williams 1990). Spanish heath has a shorter life span than manuka, however, and in the absence of fire disturbance it is replaced by it and other native species in less than 30 years (Wassilieff 1982; McQueen 1991). Druce (1957) predicted mixed stands of Spanish heath and gorse would be replaced by kamahi (*Weinmnannia racemosa*) forest in about 50 years, a similar period to that through manuka.

Hakea gibbosa (downy hakea), *H. sericea* (prickly hakea)

These two wind-dispersed needle-leaved species have fire-resistant capsules which open when burnt, effectively forming a canopy seed bank. Downy hakea was first recorded in 1937 and prickly hakea in 1883 (Webb *et al.* 1988). They are common on highly leached soils ('gumlands') in Northland where each species is more common on particular soil types (Enright 1989; Clarkson *et al.* 2011). Prickly hakea is also present on leached granitic soils in the lowland western Nelson (Esler 1961).

In Northland, these two species co-occur in shrublands with native fire-adapted species such as manuka and *Epacris pauciflora*. However, downy hakea is a smaller shrub than prickly hakea (Webb *et al.* 1988) and is more readily overtopped and replaced by manuka (author, pers obs.). Conversely, in the Kaimaumau wetland in Northland, prickly hakea is short-lived. On drier sites in the absence of fire, it is replaced by taller native species such as kanuka but because it tolerates seasonally wet areas, it can remain a permanent feature of wetter sites (Hicks *et al.* 2001). However, disturbance by fire is common in these landscapes and both hakea species are likely to be a persistent component of gumland vegetation (Enright 1989, McQueen & Forester 2000, Clarkson *et al.* 2011).

Nelson differs from Northland because fire disturbance is rare now and stands of prickly hakea commonly collapse from age and or wind-throw (Williams 1992a). It is commonly replaced where it grows in mixed stands with manuka and kanuka. In the absence of these species, soil infertility and summer drought combine to make succession slow at some Nelson sites and prickly hakea is likely to persist indefinitely (Williams 1992a).

Hakea salicifolia (willow-leaved hakea)

The tallest of the hakea species, it was first recorded in 1908 (Webb *et al.* 1988) and is now widespread in the North Island where conditions are favourable (Webb *et al.* 1988). In contrast, the only accounts of its presence in the South Island are from western Nelson (Esler 1961, Williams 1992b). The national distribution of this species appears to be restricted in part to suitabily infertile soils (author

pers. obs.).

In contrast to the other hakea species, willow-leaved hakea forms a small tree and is structurally similar to kanuka. Potentially, this additional height, combined with other physiological differences enables it to occupy a wider range of sites than the other hakea species. On the more fertile soils it occupies, willow-leaved hakea is replaced by native broad-leaved species in 50-60 years, whereas on the poorest soils, it persists for a longer, yet undefined time period (Williams 1992b).

***Lantana camara* (lantana)**

This fleshy-fruited multi-stemmed shrub was first recorded in 1912 (Webb *et al.* 1988). It is largely confined to Northland below 200 metres a.s.l. There are no accounts of it being replaced by native species although these occur with lantana on forest margins (Hill & Seawright 1983; Maseyk 1998).

***Leycesteria formosa* (Himalayan honeysuckle)**

This fleshy-fruited multi-stemmed shrub was recorded in 1878 (Webb *et al.* 1988). It is very abundant in many parts of New Zealand, especially the West Coast. In the Hutt Valley, Himalayan honeysuckle can grow as tall as bracken (*Pteridium esculentum*) seven years after fire, after which it is replaced by a low forest of karamu (*Coprosma robusta*) and mahoe (*Melicytus ramiflorus*) in much less than 50 years (Croker 1953). In Otago, where it has spread after the cessation of grazing, it reaches its maximum height in 4 years, after which it grows less vigorously when growing with bracken (Anstey 1974). Himalayan honeysuckle increased after the cessation of grazing on Banks Peninsula, but it was not expected to be long lived (Wilson 1994). Observations made in April 2009 of the localities described by Wilson (1994) indicate that the Himilayan honeysuckle has largely been replaced by mahoe (author pers. obs.).

***Ligustrum lucidum* (tree privet)**

This tall fleshy-fruited tree was first recorded in 1958 (Webb *et al.* 1988) and is now widely naturalised in the North Island, particularly from Northland to the eastern Bay of Plenty (Swarbrick *et al.* 2009). Its shade-tolerance, height, and longevity mean that it can enter native vegetation and dominate the canopy (Cameron 1990), even replacing canopy native species such as taraire (*Beilschmiedia taraire*; Fromont & King 1990). There are no studies indicating tree privet forests are likely to be replaced by native species in the foreseeable future.

***Ligustrum sinense* (Chinese privet)**

This fleshy-fruited small shrub was recorded in 1950 and is widespread from Northland to the West Coast (Webb *et al.* 1988). A study in the Waikato (Grove & Clarkson 2005) showed that growth appears to be limited primarily by light environment, although seedling shade tolerance is a factor in its spread in Auckland City (Esler 1988). Prolific invasion occurs in highly disturbed sites, particularly the edges of secondary native lowland forest, and wetland habitat across the Waikato region. It invades the margins of pine plantations in the region but does not penetrate mature stands (Denyer 2000). Chinese privet reduces the diversity of native species, which suggests that it is able to persist at a site and slow native forest succession (Grove & Clarkson 2005).

***Lupinus arboreus* (tree lupin)**

This short-lived legume was recorded in 1899 (Webb *et al.* 1988) and is now very widespread in coastal areas and riverbeds. In recent decades it has spread to hillsides in inland areas (e.g., near Waiouru in the North Island and the Buller Gorge in the South Island; author, pers. obs.). Tree lupin fixes appreciable nitrogen that is likely to impact on growth of plantation conifers (Sprent & Silvester 1973), but no studies have been made on its role in native succession. On stable sites, tree lupin persists for less than a decade and is soon replaced by other species, including native species such as flax (*Phormium* spp.) and karamu (McQueen 1993) but also non-native species including woolly nightshade (author, pers. obs.).

***Lycium ferocissimum* (boxthorn)**

This bird-dispersed spiny- and fleshy-fruited shrub was first recorded in 1897 (Webb *et al.* 1988) and grows mainly in coastal areas. McQueen (1983) considered native species regeneration beneath boxthorn was inhibited by lack of organic matter accumulation, although he did show a figure (p. 56) of karamu (*Coprosma repens*) growing within a boxthorn bush and suggested that it could ultimately outgrow the boxthorn. However, browsing of native seedling by mammals such as rabbits in dry coastal areas occupied by boxthorn may preclude this from occurring (author, pers. obs.).

***Racosperma longifolia* (Sydney golden wattle), *R. mearnsii* (black wattle)**

These two tall wattle species are reported as the most invasive of the several species present in New Zealand. While Sydney golden wattle was first recorded in 1897, black wattle was reported 100 years later (Webb *et al.* 1988). Mostly they are associated with disturbed ground and do not persist after canopy closure by native trees (Esler 1988). On very infertile gumlands in Northland where there are few if any native trees, Sydney golden wattle persists, excluding shorter native vegetation (McQueen & Forester 2000). Additionally, silver wattle (*R. dealbatum*) was recorded in the wild as early as 1870 (Webb *et al.* 1988) and is possibly the most widespread species, especially on riverbeds, but there are no studies of its role in vegetation succession.

***Rhamnus alaternus* (evergreen buckthorn)**

This evergreen shrub with abundant fleshy-fruited seeds was recorded in 1940 (Webb *et al.* 1988) and is common in coastal areas as far south as Otago (Webb *et al.* 1988). Evergreen buckthorn is particularly abundant in the Hauraki Gulf where it forms dense and persistent communities on coastal cliffs, sometimes as an understory to pohutukawa (*Metrosideros excelsa*) forest (Miller *et al.* 1994).

***Rosa rubiginosa* (sweet briar)**

This spiny fleshy-fruited shrub was recorded in 1867 (Webb *et al.* 1988) and is widespread in semi-arid parts of eastern inland South Island, particularly the upper Clutha and parts of Marlborough (Molloy 1976). Taller native species were less common than taller non-native species in sweet briar-dominated communities in the driest parts of Otago (Walker *et al.* 2003). This suggests that many sweet brier communities in harsh sites will be replaced by taller non-native species, whereas on more benign sites

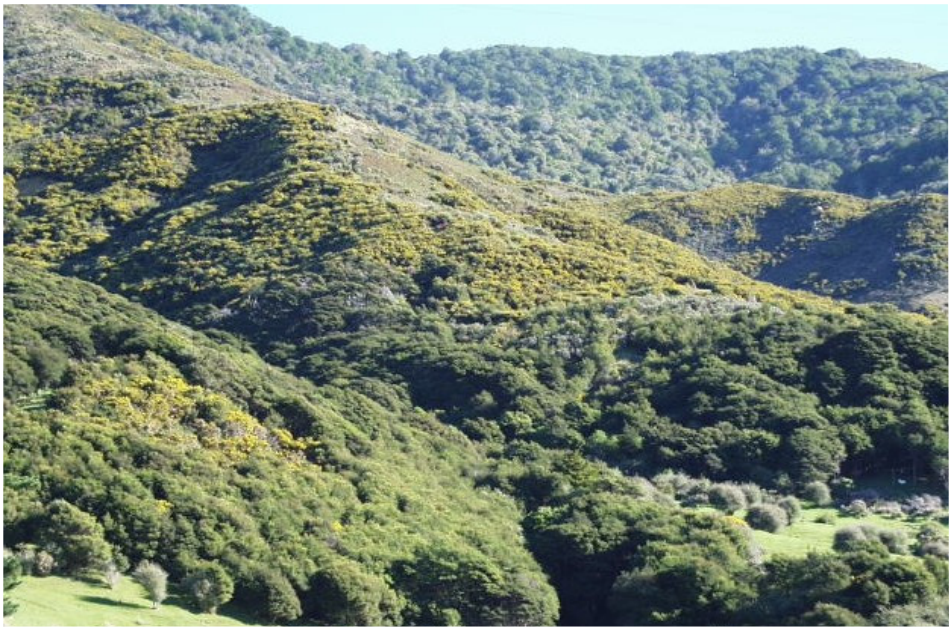

Figure 2. Succession through gorse is the most widely studied in New Zealand, as here at Nelson. There is evidence the resulting forest will be different from that developing beneath the surrounding kanuka

they will be replaced by native species including Hall's totara (Walker *et al.* 2009). Similar patterns are seen in inland Marlborough (author, pers. obs.).

Salix spp. (willows)

The main willows are crack willow (*Salix fragilis*) which spreads only vegetatively, first recorded in 1880 (Webb *et al.* 1988), and grey willow (*S. cinerea*) which spreads by wind-blown seeds, first recorded in 1925 (Webb *et al.* 1988). Willows are dominant over large areas and in most places would appear to persist (author, pers. obs.), although Wardle (1991) noted that some native species were able to establish in the understory.

On the Canterbury Plains adjacent to Bank Peninsula, 22 native bird-dispersed species were recorded from beneath willows (mainly grey willow; Pratt 1999). The non-native elderberry (*Sambucus nigra*) was most common overall. *Coprosma* spp. were the most common native species, followed by mahoe and cabbage tree (*Cordyline australis*). A few podocarp seedlings were also present but whether they will form an understory or replace the willows is unknown.

Sambucus nigra (elder)

This fleshy-fruited short-lived tall shrub or small tree was recorded in 1867 (Webb *et al.* 1988). It is common throughout New Zealand and forms distinct shrublands mainly in the drier areas of eastern South Island. It is widespread in Otago within matagouri-mingimingi (*Leucopogon fasciculatus*) associations (Walker *et al.* 2003).

On the Port Hills of Canterbury, elder replaces broom (Williams 1983). Because elder fruit are attractive to birds, more seeds of native woody species are deposited beneath elder than in adjacent bracken. The resulting seedlings have greater survival beneath elder because of reduced competition from bracken and grass (Voyce 1998). As a result, there is some evidence that elder eventually dies

out and is replaced by mahoe (Williams 1983).

Solanum mauritianum (woolly nightshade)

This short-lived fleshy-fruited shrub was recorded in 1883 (Webb *et al.* 1988). It is particularly common in the northern regions of the North Island, where it often replaces gorse and other low scrub (author, pers. obs). No replacement of woolly nightshade by native species was observed in Auckland City by Esler (1988). There is some evidence for possible allelopathic effects on native species (van de Bosch *et al.* 2004), but whether this influences their establishment beneath woolly nightshade is unknown.

Ulex europaeus (gorse)

This spiny-leaved shrub with very long-lived seeds was first recorded in 1867 (Webb *et al.* 1988). Gorse has long been widespread in New Zealand and is well-studied (Figure 2), although it has still not reached the limits of its potential range. Gorse rapidly achieves stand dominance over more browse-susceptible native shrubs. Gorse is a relatively short-lived shrub with a maximum age of 47 years in New Zealand (Druce 1957), although under equable conditions near sea level it may reach a maximum of only 22 years before collapsing (Williams 1992a). In mild conditions on former forested sites and in the absence of fire, gorse is replaced by native broadleaved species in two to three decades. This succesional trajectory has been observed in the southern North Island (Druce 1957; Esler 1978; Bagnall 1981; Oates 1988), northern South Island (Wassilieff 1982; Sullivan *et al.* 2007), and Banks Peninsula (Wilson 1994). In contrast, the process seems much slower in the cooler climate of Dunedin (Lee *et al.* 1986; Ogle-Mannering 1995). However, although grazing animals were absent from the Taita (Lower Hutt, southern North Island) and Banks Peninsula studies mentioned above, they may have limited the growth of broadleaved species in the Dunedin stands. In a study examining the establishment of native woody seedlings in a Dunedin gorse succession, high densities of broadleaved species were found in the old stand, but stand age and proximity to seed source could not be differentiated because the absence of replication (Ogle-Mannering 1995).

On former beech (*Nothofagus* spp.) forest sites in Wellington early gorse dominance led to a five-finger (*Pseudopanax arboreus*) canopy in less than 20 years (Druce 1957). In contrast, where manuka was the post-fire dominant, manuka was predicted to remain dominant for at least 50 years (Druce 1957), with five-finger merely as an understory. These differences are reflected in overall vegetation composition (Sullivan *et al.* 2007).

Gorse is replaced by kanuka where they establish contemporaneously on Banks Peninsula (Wilson 1994). There is strong evidence, for reasons yet to be investigated, that *Nothofagus* species will not establish in gorse on Banks Peninsula even when it grows on former *Nothofagus* soils (Oates 1988; Wilson 1994). On drier sites in the Kaimaumau wetland and on adjacent dunes in Northland, gorse is replaced by Sydney golden wattle (Hicks *et al.* 2001) and in Nelson there is a large area of mixed gorse and broom being replaced by Japanese cherry (*Prunus serrulata*; Figure 3, author, pers. obs.).

Discussion

About two thirds of the 36 non-native woody dicotylous shrubs and trees discussed here that form dense patches

on the New Zealand landscape have been studied or commented upon regarding their persistence or role in vegetation succession; broom, buddleia, Chinese privet, Darwin's barberry, elder, evergreen buckthorn, gorse, hakea species, Himalayan honey suckle, Spanish heath, sweet briar, wattles, and willows. These accounts are derived mainly from casual observations, or "space for time" studies (e.g., Croker 1953; Williams 1983; Smale 1990). Rarely have observations been repeated at the same site over time, as is the case for gorse on Banks Peninsula (Wilson 1994; Bellingham *et al.* 2005), or the many successional studies involving exclusively native species (Wardle 1991).

For species that are described as dominating the canopy their observed or predicted replacement by native forest can take place in 50-100 years under favourable soil and climatic conditions (see individual species for references; e.g., gorse, Himalayan honey suckle, Spanish heath, willow-leaved hakea). Many other species are reported as having native seedlings beneath the canopy but their replacement by native species is only speculative.

A question that should be considered by land managers is to what extent non-native woody species influence future forest composition. This appears initially to be partly dependent on their relative density, compared with native species, at time of establishment. For example, although manuka and kanuka do not establish within dense gorse, if they establish with it, they replace gorse (author, pers. obs.). Similarly, Druce (1957) predicted several mixed native and non-native successional communities would lead to the same vegetation as purely native successions. What the native : non-native ratio is that ensures a subsequent native vegetation remains an open question, but the range of potential outcomes from a single non-native woody species component at a site is best documented for buddleia.

Buddleia in the Urewera region was the next documented species after gorse (Druce 1957) whereby native vegetation replaced a non-native species. Where the non-native buddleia was the initial coloniser, it was replaced by an indigenous species faster than when a native species (kanuka) was initially present (Smale 1990). The differences in the speed at which the colonisers were replaced arose primarily from the shorter lives of buddleia and gorse compared with manuka and kanuka. However, it is not only the speed of non-native species replacement that needs to be considered, but also the potentially long-term differences in vegetation trajectories (Sullivan *et al.* 2007). The potential for structural differences in the crowns of manuka/kanuka compared with gorse contributing to such potential differences were discussed for gorse by Williams & Karl (2002). Similarly, the rapid transition from dense buddleia to dense mixed hardwood without a period of "shade-house-like" kanuka dominance (Smale 1990) may have consequences for future forest composition.

Most of these hypotheses are based on "space for time" studies and only in the case of the long-term Banks Peninsula studies (Wilson 1994) is there direct evidence of such longer-term differences. Here, gorse is not replaced by beech on former beech sites, but by mixed-hardwoods. This difference may also be related in a similar way to the structural differences on manuka scrub and gorse scrub but it may also relates to the limited dispersal potential of beech (Wardle 1991) and the very different soil mycorrhizal relationships of beech and gorse (beech lacks the nitrogen-fixing rhizobium nodules of gorse); certainly these questions warrant further investigation.

Figure 3. Several species of flowering cherry are becoming invasive; in this case *Prunus campanulata* competing with native species such as mahoe and five finger emerging through old stands of gorse and broom in Nelson City.

Amongst successions leading to native vegetation, not all progress directly from the first post-disturbance non-native species to native species dominance. On parts of Banks Peninsula, elder is the dominant secondary species following broom (Williams 1983), even in an environment where native bird-dispersed shrubs and a corresponding seed rain are common on the landscape (Voyce 1998). This presumably reflects a relatively unfavourable environment for native woody species establishment under degenerating broom stands, compared with more moist environments under native successional species, as Trass (2000) found on the central Volcanic Plateau.

Elder is not the only non-native species occupying this secondary position but because it is relatively short-lived, the succession can be observed. Both barberry species and hawthorn frequently invade mixed scrub with a high gorse component, but here there has been insufficient time to observe the next vegetation stage (McQueen 1993). Because both barberry (McAlpine & Jesson 2007) and hawthorn (Williams & Buxton 1986) are unable to regenerate beneath a tall canopy, they are likely to be succeeded by shade-tolerant native species where propagules are available. It has been suggested this may be broadleaf in parts of montane Canterbury (Williams *et al.* 2010). Dense patches of broadleaf seedlings and saplings have also been observed beneath old rowan (*Sorbus acuparia*) stands in Chatterton Creek, on the Hanmer Range, North Canterbury (author, pers. obs.) and McQueen (1993) pointed to the more important role of broadleaf in the cooler climate of Dunedin.

Only rarely have authors specifically noted non-native species being likely to persist for the foreseeable future. Examples include evergreen buckthorn in

coastal Auckland (Miller *et al.* 1994), Sydney golden wattle in Northland gumlands (McQueen & Forester 2000), and tree privet (Swarbrick *et al.* 2009). The replacement of sweet brier by conifers and other tall non-native species such as sycamore (Walker *et al.* 2003, author pers. obs.) will likely result in non-native species dominance for a very long time.

Several other non-native bird-dispersed species such as barberry, *Cotoneaster* spp., boneseed, *Elaeagnus* spp., firethorn (*Pyracantha angustifolia*), lantana, rowan, tree privet, and wild cherry (*Prunus* spp.) play a similar role to Darwin's barberry and hawthorn in invading post-disturbance vegetation, but there appears to be little or no written accounts of their successional role. Some species have probably not been abundant for sufficient time for their replacement by native species to have occurred, for example, Japanese cherry, first recorded in 1982; and firethorn, first recorded in 1958 (Webb *et al.* 1988) and now abundant in the central North Island (author, pers. obs.). Boneseed, although first recorded in 1870 (Webb *et al.* 1988) and now extensive on hills around Wellington (McAlpine *et al.* 2009), was largely confined to coastal bluffs some 40 years ago (author, pers. obs.).

The absence of extensive stands cannot explain the lack of accounts for other species such as barberry, *Elaeagnus* spp., lantana, and sycamore; all of which have been abundant in many regions for decades. Whether insufficient time explains Esler's (1988) observations concerning the absence of native species beneath woolly nightshade remains to be seen.

Aside from those species mentioned which appear to monopolise their sites indefinitely wherever they occur (e.g., tree privet) there are some that do so only in some situations. The most widespread species of this group are the leguminous shrubs broom and gorse. Disturbance by substrate instability (cliffs, riverbeds) and fire are widely recognised causes of the persistance of these species. Although broom fixes nitrogen that may be taken up by associated seedlings, competition for moisture is likely to outweigh the benefits of the additional nitrogen on dryland sites (Watt *et al.* 2003). The absence of taller woody plants propagules may also be a factor in apparent self-perpetuation of broom in parts of Marlborough such as in the Clarence Valley (author, pers. obs).

Summary

Thirty-six species, or species groups, of non-native dicotyledonous woody plants are now conspicuous on the New Zealand landscape, in patches of greater than 80% cover and that exceed 0.25 ha in area. This about twice the number reported about 20 years ago (McQueen 1993) and attests to the rapid changes occurring. Attitudes to these plants range from considering them pests to being valued for their role in secondary succession leading to native vegetation. An up-to-date summary of the available information on their role in succession is provided here, supplemented by the author's unpublished observations. Twenty-seven of these plants have at least one reference but the comments are often very general and inconclusive as to whether the species is being replaced by native species. Of the 36 species, 14 are described as being replaced by native species in some circumstances (*Buddleja davidii*, *Calluna vulgaris*, *Cytisus scoparius*, *Erica lusitanica*, *Hakea gibbosa*, *H. salicifolia*, *H. sericea*, *Leycesteria formosa*, *Lupinus arboreus*, *Racosperma longifolia*, *R. mearnsii*, *Rosa rubiginosa*, *Sambucus nigra*, and *Ulex europaeus*). A further 8 species are reported to have native seedlings beneath

the canopy, but whether these will replace the non-native species remains to be seen (*Acer pseudoplatanus*, *Berberis darwinii*, *B. glaucocarpa*, *Chrysanthemoides monolifera* spp. *monilfera*, *Crataegus monogyna*, *Lycium ferocissimum*, *Salix cinerea*, and *S. fragilis*). The remaining 14 species have no records of either being replaced or having native species beneath their canopies. A few of these are short-lived shrubs that are probably replaced by native species in some circumstances, only this has not yet been noted (e.g., *Lantana camara* and *Teline monspessulana*). However, there is a paucity of knowledge in regards to the remainder (*Cotoneaster* spp., *Elaeagnus x reflexus*, *Ligustrum lucidum*, *L. sinense*, *Paraserianthus lophantha*, *Prunus* spp., *Pyracantha angustifolia*, *Racosperma dealbata*, *Rhamnus alaternus*, *Rhododendron ponticum*, *Solanum mauritianum*, and *Sorbus aucuparia*). Two of these species are reported as likely to be persistent for the foreseeable future (*Ligustrum lucidum* and *Rhamnus alaternus*) and this also applies to the hard-seeded legumes in frequently disturbed habitats.

There is clearly a multitude of outcomes across a wide range of habitats following invasion by non-native woody species. Several of these outcomes have been described as being dependant on the relative densities of the native and non-native species at the earliest stages of vegetation succession. It would be interesting for managers to know what the minimum densities of non-native species were for their potential to deflect the successions away from those that might occur in purely native plant communities. This is has been termed the impact threshold (e.g., Gooden *et al.* 2009). Because many of the longer-lived species described have begun to form extensive stands for a shorter time than their life span (cf. gorse), it is opportune to establish a series of permanent observation points, preferably with and without grazing. We would then be less dependant in the future on "space for time" studies in understanding the changes that are occurring on the New Zealand landscape and have a firmer basis for categorising some of these species as pests or desirable plants in a range of circumstances.

Acknowledgements

Thanks to Debra Wotton for locating several unpublished references. Much of this summary was compiled prior to my retirement from Landcare Research. Two anonymous referees and the associate editor (Frank Burdon) made many helpful suggestions to the text.

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